

## A NEW SATANOPERCA SPECIES (TELEOSTEI, CICHLIDAE) FROM THE AMAZON RIVER BASIN IN BRAZIL

by

Sven O. KULLANDER (1) and Efrem Jorge Gondim FERREIRA (2)

**ABSTRACT.** - *Satanoperca lilith* n. sp. is described from many localities especially in the Rio Negro drainage, but also from the Branco, Japurá, Trombetas, Solimões, Amazonas, Aripuanã, Uatumã, Canumã and Tapajós drainages in Brazil. The species reaches 255 mm SL and is distinguished from the most similar species, *Satanoperca daemon* (Heckel), by having only one instead of two dark blotches on the side.

**RÉSUMÉ.** - *Satanoperca lilith* n. sp. est décrite d'après des exemplaires provenant de plusieurs localités du bassin du Rio Negro, du Branco, du Japurá, du Trombetas, du Solimões, de l'Amazonas, de l'Aripuanã, de l'Uatumã, du Canumã et du Tapajós au Brésil. L'espèce peut atteindre 255 mm en longueur standard et se distingue de l'espèce voisine, *Satanoperca daemon* (Heckel), par la présence d'une seule, et non de deux taches sombres sur les flancs.

**Key-words :** Cichlidae, *Satanoperca lilith*, Amazon R., ASW, Brazil, New species.

Before the revision by Gosse (1976), the taxonomy of the South American cichlid genus *Geophagus* Heckel, 1840 had for a long time been in a state of extreme confusion, involving a large number of nominal genera and species for which no adequate diagnoses were available. Gosse (1976) recognized 10 valid species of *Geophagus* and assigned some species formerly identified as *Geophagus* species to other genera. It seems, however, that *Geophagus* sensu Gosse includes distinct lineages which should be recognized as separate genera, and that many more species exist.

Kullander (1986) distinguished *Satanoperca* Günther, 1862 as a valid genus comprising *S. jurupari* (Heckel, 1840), *S. daemon* (Heckel, 1840) and *S. acuticeps* (Heckel, 1840), which were included in *Geophagus* by Gosse. *Satanoperca leucosticta* (Müller & Troschel, 1849) and *S. pappaterra* (Heckel, 1840), treated as synonyms of *S. jurupari* by Gosse, are also valid *Satanoperca* species. Kullander (1986) indicated the existence of other, undescribed species.

Reexamination of some of Gosse's material of *S. daemon* shows that most of it belongs to an undescribed, widely distributed species. His *S. acuticeps* material includes also *S. daemon* and the undescribed species, and it is evident that the group of *Satanoperca* species with one to three black blotches on the side requires revision. The purpose of this paper is to describe the *Satanoperca* species until now confused with *S. daemon* and show how it can be distinguished from other *Satanoperca* species.

### MATERIAL AND METHODS

All lengths are standard length (SL) unless otherwise stated. Methods of measuring follow Kullander (1980a, b ; 1986). Frequencies are given in parenthesis after each count. Stomach content analyses were made according to Ferreira (1984)

(1) Department of Vertebrate Zoology, Swedish Museum of Natural History, PO Box 50007, S-104 05 Stockholm, SWEDEN.

(2) Departamento de Biologia Aquática e Limnologia, Instituto Nacional de Pesquisas da Amazônia, CP 478, 69 000 Manaus (AM), BRAZIL.

and are based on fishes captured from several localities in the Rio Negro. Feeding index was calculated as  $(MV \times RO / \sum (MV \times RO)) \times 100$ , where MV is mean volume, RO relative occurrence.

Specimens reported on in this paper are deposited at the following institutions : Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA), Institut royal des Sciences Naturelles de Belgique, Brussels, Belgium (ISNB), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Naturhistorisches Museum Wien, Vienna, Austria (NMW), Swedish Museum of Natural History, Stockholm, Sweden (NRM), National Museum of Natural History, Washington, DC, USA (USNM).

Comparative material of *Satanoperca daemon* includes the following, on which the distribution map, Fig. 4, is based.

Venezuela, Rio Negro drainage : USNM 269311. 1. Caño Chola where crossed by road from San Carlos to Solano : USNM 269336. 12. Lagoon NE airport of San Carlos : USNM 269365. 10. Caño Manu, tributary of Rio Casiquiare ca 250 m upstream from Solano. Rio Orinoco drainage : USNM 269334. 3. Laguna Provincial, ca 20 km N Puerto Ayacucho : ISNB 15226. 1. Between San Fernando de Atabapo and Rio Casiquiare.

Colombia, Rio Orinoco drainage : NRM THO/1972104.3142. 3. Finca Boca de Guarrojo, caño no 2 : NRM THO/1972103.4138. 5. Finca Boca de Guarrojo, estero close to laguna no 1 : NRM THO/1972100.3144. 1. Finca Boca de Guarrojo, larger laguna : NRM THO/1977179.8168. 1. Cerro Mavecuri.

Brazil, Rio Negro drainage : ISNB 17415. 8. Igarapé right bank affluent of R. Uaupés at Trovão : NMW 23123. 1. Holotype. Marabitanas.

#### *SATANOPERCA LILITH* N. SP.

(Figs 1-5, Tables I-III)

*Geophagus daemon* ; (in part) Steindachner 1875, p. 118 (descr.). (in part) Gosse 1976, p. 44 (descr.), Pl. II, Fig. A (lower pharyngeal tooth plate).

*Geophagus acuticeps* ; (in part) Gosse 1976, p. 60 (descr.).

**Diagnosis :** a large *Satanoperca* species (reaching 255 mm), with 29-31 scales in a lateral row and 20 circumpeduncular scale rows. Distinguished from the most similar species, *S. daemon*, by colour pattern, having a single dark blotch on the side, situated across or entirely dorsal to the upper lateral line. *Satanoperca daemon* has two flank blotches, both situated below the upper lateral line. See also Table I for summary of diagnostic characters of *Satanoperca* species.

#### Examined specimens :

**Holotype** : MZUSP 33003. 101.2 mm standard length. Brazil, Estado do Amazonas, Rio Negro drainage, Urumari, praia ( $0^{\circ}0'3''S$   $63^{\circ}30'W$ ). 6 October 1979. Leg. Michael Goulding.

#### Paratypes (all from Brazil) :

Rio Trombetas drainage (Estado do Pará) : ISNB 758. 2, 193.2-219.0 mm. Jamari, igarapé above Lago Jamari on right bank of R. Trombetas. 1 Dec. 1964. Léopold III and J.-P. Gosse (Sta. 135).

Rio Negro drainage (Estado do Amazonas) : ISNB 759. 3, 61.4-71.6 mm. Arquipélago das Anavilhas, left bank igarapé tributary to R. Negro. 18 Nov. 1967. Léopold III and J.-P. Gosse (Sta. 179). NRM MEL/1923477.3092. 1, 232.0 mm. Small white water river near Manaus. 25 Nov. 1923. D. Melin, A. Vilars, A. Roman. NRM MEL/1923475.4178. 1, 62.1 mm. Small white water river near Manaus. 23 Nov. 1923. D. Melin, A. Vilars, A. Roman. MZUSP uncat. 1. 72.6 mm. Paraná do Marauá. Jan. 1987. M. Goulding (K26-80).

Rio Uatumã drainage (Estado do Amazonas) : INPA 1542. 1, 200.0 mm. Lower R. Uatumã. Apr. 1985. Equipe de Ictiologia do INPA.

**Non types** (all from Brazil) : The following material was identified as *S. lilith*, but no data was taken. Largest specimen 255 mm (MZUSP 33007).

Table I : Characters useful for distinguishing *Satanoperca species*. The *S. jurupari* group includes several undescribed species which agree in the characters considered. Ll 1 : upper lateral line : Ll 2 = lower lateral line.

	<i>S. acuticeps</i>	<i>S. daemon</i>	<i>S. liliith</i>	<i>S. jurupari</i> group
Maximum size (mm SL)	150	230	255	160
Scales in a lateral series (boldface = mode)	27-28	29-30	29-30-31	27-28
Dorsal fin modal count	XIII.12	XIV.13	XIV.13	XV.10 or XVI.9
Circumpeduncular scale rows	16	20	20	16
Vertebral count mode	14+14	16+14	16+14	15+14
Number of flank blotches	3	2	1	0
Position of flank blotches	above L12	below L11	on/above L11	----
Position of caudal ocellus on dorsal lobe	ventral	middle	middle	dorsal
Snout tip	at L12 level	below L12	below L12	below L12
Lower lip fold	continuous	interrupted	interrupted	interrupted
Filamentous free rays in dorsal fin	Yes	Yes	Yes	No

Rio Solimões drainage (Estado do Amazonas) : MZUSP 33016. 1. R. Japurá, Lago Amanã. R. Best (34). ISNB 15895. 1. Small igarapé tributary to R. Jacitara, Lago Grande do Manacapuru. 12 Nov. 1962. Léopold III and J.-P. Gosse (Sta. 9). ISNB 15896. 5. Small igarapé affluent of R. Caraná, Lago Grande do Manacapuru. 13 Nov. 1962. Léopold III and J.-P. Gosse (Sta. 11). MZUSP uncat. 1. Lago Janauacá and surroundings. Sep. 1976-Jan. 1977. Alpha Helix.

Rio Negro drainage (Estado do Amazonas) : MZUSP 33001. 5. R. Marié, Lago Curumuru. 17 Oct. 1979. M. Goulding. MZUSP 33000. 1. R. Arirará near mouth, praia. 6 Oct. 1979. M. Goulding. MZUSP 32999. 1. R. Arirará near mouth, igapó. 28 May 1979. M. Goulding. MZUSP 33004. 1. Mandiquié, jarazal igapó. 8 Oct. 1979. M. Goulding. MZUSP 33013. 19. Arquipélago das Anavilhanas, igapó. Jan. 1980. MZUSP 33007. 12. Ilha Buiu-açu, lago. 6 Feb. 1980. M. Goulding. MZUSP 33011. 3. R. Cuiuni near mouth, igapó. 3 Jun. 1979. M. Goulding. MZUSP 33014. 4. São Pedro, igapó. 23 May 1979. M. Goulding. MZUSP 33002. 4. Ilha Tamaquaré, igapó. 7 Feb. 1980. M. Goulding. MZUSP 33015. 17. Arquipélago das Anavilhanas, igapó. Oct. 1979. M. Goulding. MZUSP 33005. 10. Mouth of R. Urubaxi, swamp. Feb. 1980. Leg. M. Goulding. MZUSP 33012. 1. Below R. Daraá, rocky pool. 16 Feb. 1980. M. Goulding. MZUSP 33009. 1. Below R. Daraá, woody shore. 12 Feb. 1980. M. Goulding. MZUSP 33006. 11. Ilha Cumuru, beach. 1 Feb. 1980. M. Goulding. MZUSP 33010. 12. Barcelos, island lake. 29 Feb. 1980. Leg. M. Goulding. MZUSP uncat. 1. R. Marauá near mouth. 14 Oct. 1979. M. Goulding. MZUSP uncat. 4. São João. 4 Oct. 1979. M. Goulding. ISNB 1008. 1. Lago Janauari. / 1865-1866. Thayer Expedition. / ISNB 17414. 2. Igarapé tributary to left bank of R. Negro in the Arquipélago das Anavilhanas. 19 Nov. 1967. Léopold III and J.-P. Gosse (Sta. 180). NMW 23098-23013 (pt). 3. Manaus. / 1865-1866. Thayer Expedition. NMW 23015. 1. Lago Janauari. / 1865-1866. Thayer Expedition. / NMW 23029. 1. Lago Janauari. / 1865-1866. Thayer Expedition. / MZUSP 6850. 1. Igarapé no 2 tributary of Igarapé Tarumázinho. 18 Nov. 1967. EPA. MZUSP 6738. 3. R. Negro, vicinity of Manaus. 19-23 Nov. 1967. EPA. MZUSP 6791. 2. Igarapé Tarumázinho, affluent no 1, Manaus. 17-18 Nov. 1967. EPA.

Rio Amazonas drainage (Estado do Amazonas) : ISNB 17416. 4. Lago Laginho at Vila Amazônia on the right bank of R. Amazonas at confluence with Paraná do Ramos, downstream of Parintins. 15 Dec. 1964. Léopold III and J.-P. Gosse (Sta. 136). NMW 24204-24205. 2. Lago Máxima. / 1865-1866. Thayer Expedition. / MZUSP 7490. 4. Mun Silves, igarapé tributary to R. Sanabani. 7 Dec. 1967. EPA. NMW 23129. 1. Obidos / 1865-1866. Thayer Expedition.

Rio Tapajós drainage (Estado do Pará) : ISNB 15897. 27. Santarém, Igarapé Mapiri. 30 Nov. 1963. G. Marlier (Sta. 145). MZUSP 32998. 6. Pederneiras, rocky pool. 24 Oct. 1983. M. Goulding. MZUSP uncat. 2. Aveiro, Igarapé Açu. 30 Oct. 1970. EPA. MZUSP 25186. 5. Igarapé at Km 55 of BR 230, Parque Nacional da Amazônia (PARNA). 15-31 Jul. 1979. J.C. Oliveira. MZUSP 8422. 5. Mun Santarém, Alter do Chão, Igarapé Jacundá. 23 Dec. 1967. EPA. MZUSP 8456. 17. Mun. Santarém, Alter do Chão, Lago Jacundá. 23 Dec. 1967. EPA. MZUSP 8503. 20. Mun Santarém, igarapé left bank tributary to R. Mapiri. 25 Dec. 1967. EPA.

Rio Trombetas drainage (Estado do Pará) : MZUSP 32997. 12. Cuminá, channel. Oct. 1983. M. Goulding. ISBN 17412. 1. Igarapé Matapi at Lago Matapi, right bank of R. Trombetas, downstream of Lago Jamari. 2 Dec. 1964. Léopold III and J.-P. Gosse (Sta. 136). NMW 24206. 1. R. Trombetas. /1865-1866. Thayer Expedition. / MZUSP 15557 pt. 4. Reserva Biológica de Trombetas, Cachoeira da Serrinha, Lago Jacaré. 25 Jul. 1979. R.M.C. Castro. MZUSP uncat. 2. Lago Jacaré. 29 Sept. - 13 Oct. 1965. Exped. Depto. Zoologia and Museu Goeldi. MZUSP 5586. 2. Oriximiná, Lago Parauaçu. 7 Feb. 1967. EPA. MZUSP 8217. 5. Oriximiná, Lago Jacupá. 17 Dec. 1967. EPA.

Rio Canumã drainage (Estado do Amazonas) : MZUSP 7077. 1. R. Canumã. 28-29 Nov. 1967. EPA.

Rio Aripuanã drainage (Estado do Amazonas) : INPA 1540. 2. Igarapé do Castanhais. 22 Aug. 1976. Equipe de Ictiologia do INPA.

Rio Branco drainage (Território do Roraima) : INPA 1541. 2. Pool isolated by bueiro on road Boa Vista-Paredão, ca Km 30. 7 Oct. 1986. E. Ferreira, G. Mendes.

Imprecise locality : NMW 23130-23131. 2. Amazonas Gebiet. 1908. Steindachner ded.

**Description :** Based on the holotype and nine paratypes. See Fig. 1 for general aspect and Table II for summary of morphometric data.

Elongated; laterally compressed, especially dorsally; back and nape keeled. Dorsal contour more arched than the ventral; deepest at origin of pelvic fins; chest flattened; contour in anterior view broadly rounded ventrally, pointed dorsally.

Head moderately deep. Predorsal contour about straight to just before dorsal fin but decurved above mouth and with a slight elevation in front of the eye; prepelvic contour less steep, straight. Orbit below predorsal contour, in posterior and dorsal halves of head; most of it above level of gill cleft in large specimens. Snout long, in lateral aspect broadly triangular. Mouth little wider than interorbital space; situated far below level of eye, near ventral body outline; lower jaw slightly prognathous; maxillary tip exposed, reaching caudad to little behind nostril; ascending processes of premaxilla reaching about as far as maxilla. Nostril about halfway between orbit and snout tip. Operculum a little more than twice as deep as long. Preoperculum entire; supracleithrum entire in holotype, in paratypes serrated beneath the lateralis canal opening. Lip folds moderately wide; upper lip fold continuous, lower lip fold interrupted near symphysis.

Flank scales ctenoid. Scales in a lateral row 29(2), 30(7), 31(1). Predorsal scales cycloid, small, the largest about half as large as anterior flank scales. Preventrally and in advance of a line between pelvic and pectoral fin bases the scales are small, with marked forwards size decrease; posterior prepelvic scales about half the size of anterior flank scales, but anterior one-third size of posterior. Chest scales ctenoid, prepelvic scales cycloid (interpelvic scales ctenoid in 232 mm specimen), posteriorly in a median row but especially rostral to naked pit opposite cleithral tips tightly packed and irregular in arrangement. Abdominal scales ctenoid. Cheek scales about half the size of anterior flank scales along lacrimal and infraorbitals, below much smaller. Cheek naked below a line continuing oral lacrimal margin caudad, and just above that area a zone of particularly small scales; all cheek scales cycloid and more or less embedded; counted as horizontal rows 6(1), 7(1), 8(3), 9(4) or 10(1). Opercular scales cycloid, of varying sizes, not larger than a half anterior flank scale, arrangement irregular. Subopercular scales irregular, in about two or three rows, outer margin narrowly naked; largest scales about half size of anterior flank scales. Interopercular scales one to three, small, cycloid and deeply embedded, next to suboperculum. Preoperculum naked. Circumpeduncular scale rows 20 (9 above and 9 below lateral line).

Upper lateral line at 5 1/2-6 1/2 (initially) to 2 1/2-3 1/2 (at end) scales distance from dorsal fin. Lateral lines with tube bearing scales only: 19/12(1), 19/13(1), 19/14(1), 20/12(3), 20/13(1), 21/12(1), 21/13(1), 21/14(1); two scales

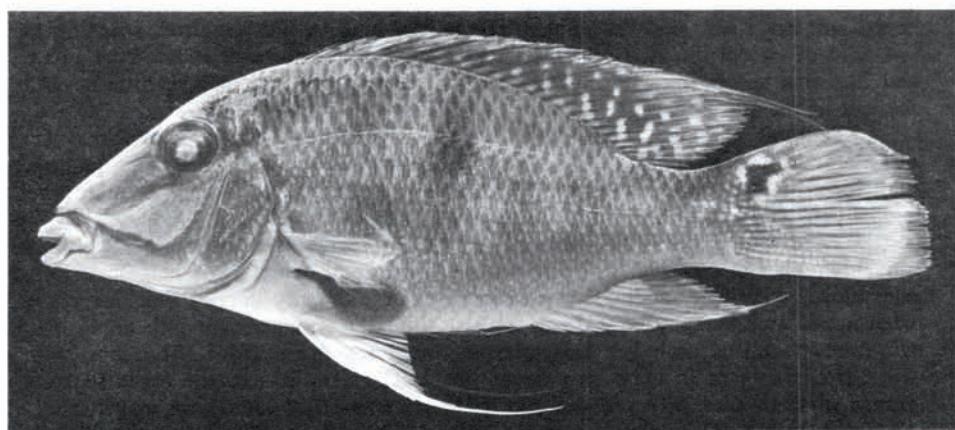


Fig. 1 : *Satanoperca lilith*, holotype, MZUSP 33003. 101.2 mm SL, from Urumari, Rio Negro drainage.

Table II : Morphometry of type series of *Satanoperca lilith*. Measurements in mm ; range and mean  $\pm$  standard error of the mean in per cent of SL.

	Measurements in mm										in per cent of SL	
	SL	61.4	62.1	65.3	71.6	72.6	101.2	193.2	200.0	219.0	232.0	Range
Head length	21.8	22.2	23.3	26.2	25.5	34.3	63.4	64.0	71.9	76.0	32.0-36.6	34.3 $\pm$ 0.51
Snout length	8.5	9.5	9.6	11.6	9.5	16.4	33.5	31.5	38.4	37.5	13.1-17.5	15.6 $\pm$ 0.45
Body depth	22.3	22.9	24.1	26.8	28.2	40.1	73.0	72.3	76.4	83.2	34.9-39.6	37.1 $\pm$ 0.45
Orbital diameter	7.3	7.4	7.6	8.2	8.5	9.9	16.2	18.5	18.1	20.1	8.3-11.9	10.3 $\pm$ 0.50
Head width	9.7	9.5	10.3	11.0	11.2	14.1	26.0	27.9	30.0	31.5	13.5-15.8	14.6 $\pm$ 0.31
Interorbital width	5.2	5.2	5.5	6.3	6.1	8.5	16.7	17.6	19.8	21.8	8.4-9.4	8.7 $\pm$ 0.11
Preorbital depth	6.6	7.0	7.5	8.4	8.7	13.0	27.0	27.0	29.6	32.2	10.7-14.0	12.5 $\pm$ 0.38
Caudal peduncle depth	8.2	8.4	9.3	9.9	9.9	14.7	26.5	27.4	28.2	31.7	12.9-14.5	13.7 $\pm$ 0.14
Caudal peduncle length	8.5	9.7	9.3	10.4	10.2	14.1	31.5	30.3	31.1	36.4	13.8-16.3	14.8 $\pm$ 0.27
Pectoral fin length	19.3	20.3	21.3	24.5	23.8	33.0	63.3	69.2	70.0	82.7	31.4-35.6	33.1 $\pm$ 0.41
Pelvic fin length	21.4	19.1	17.3	20.5	26.9	45.2	76.1	95.1	97.0	125.6	26.5-54.1	38.8 $\pm$ 2.82
Last dorsal spine length	11.8	11.3	12.9	14.5	15.4	19.4	31.8	37.6	35.7	43.9	16.3-21.2	18.8 $\pm$ 0.49

continuing lower lateral line on caudal fin, which also has additional series of tubed scales between rays D3-D4 (1-4 scales) and rays V4-V5 (4-11 scales).

Caudal fin with a basal convex layer of scales continuing body squamation, a few interradial scales between median rays (less than one-fourth of fin scaled) ; along fin margins small cycloid densely packed scales (marginally more than half of fin scaled).

Dorsal fin origin above opercular margin ; spines steadily increasing in length to the last which little more than 4-6 times the length of the first ; lappets with long free posterior margin, pointed, tips reaching slightly beyond spine tips. Soft dorsal fin basically rounded, but in specimens over 100 mm soft rays 3-5 or 6 free and produced, reaching beyond middle of caudal fin ; otherwise the soft dorsal fin extends only little beyond the caudal fin base as in young. D. XIII.13(1), XIV.12(1), XIV.13(4), XIV.14(2), XV.12(1), XVI.9(1). First anal spine inserted opposite second

dorsal soft ray ; soft anal fin pointed, second ray longest, not produced, reaching to one-third of caudal fin. A. III.8(9), III.9(1). Caudal fin truncate or subtruncate ; 71.6 and 72.6 mm specimens with rays D6 and D7 forming a point reaching little beyond the rest of the fin.

Pectoral fin long, pointed, third ray longest, reaching to above anal fin origin to third anal spine. P. 14(3), 15(7). Pelvic fin pointed ; first ray longest, with long filament reaching to anal fin origin in young, to beginning or middle of caudal peduncle in the largest specimens.

Teeth simple, conical, pointed, of uniform size. Lower jaw teeth freely movable, upper more fixed. In lower jaw more than half of each jaw half posteriorly edentulous, anteriorly moderately packed teeth in a broadly curved line, leaving a wide naked area symphysially. In upper jaw similarly arranged, but little more than two-thirds to all of each jaw half toothed. Small specimens (61.4-101.2 mm) with wide, irregular gaps in upper jaw dental arcade that may in extreme cases separate groups of teeth anteriorly and posteriorly. Specimens 101.2-232.0 mm may have 1-12 inner teeth close to the symphysis in each lower jaw half ; specimens 219.0-232.0 mm have 1-4 inner teeth anteriorly in each upper jaw half. Number of teeth in the only or outer row increasing with size ; upper/lower jaw teeth arranged according to increasing SL and with jaw halves separated by a +, are for specimens 61.4-232.0 mm : 8+9/7+4, 15+10/14+14, 14+12/10+10, 15+18/13+13, 9+10/9+10, 19+20/12+15, 25+22/15+17, 28+28/15+16, 21+26/18+19, 28+34/19+16.

Gill rakers externally along first ceratobranchial 18(1), 19(4), 20(3), 21(2). A paratype, 71.6 mm, examined for gill arch structures (Figs 2-3). On first gill arch a pharyngobranchial and three medial epibranchial conical gill rakers ; 11 gill rakers along the margin of the lobe, flattened, widened distally, base narrow ; a broad digitiform gill raker in the angle ; three upper short, rostrad directed blunt ceratobranchial gill rakers and 17 short, round-tipped, chiefly laterad pointing lower ceratobranchial gill rakers ; the five anteriormost gill rakers are rudimentary. Except for the posteriormost, all ceratobranchial gill rakers attach to the skin fold over the basal part of the gill filaments, instead of to the skin over the ceratobranchial. All ceratobranchial gill rakers form the ends of low transverse ridges, opaque with white granules chiefly in cross-rows ; these ridges do not ascend the crest of the median dorsal ridge along the gill arch. On the internal face, there are 20 ceratobranchial gill rakers on the ventral margin, or on the skin fold below ; the lowermost rudimentary, the others with long, lanceolate tip connected basally with transverse soft ridge, reaching up to the dorsal margin of the medial soft ridge ; nine epibranchial gill rakers similar, but running across the lobe at some distance from the margin. All gill rakers are smooth. The epibranchial lobe is about as deep as the epibranchial is long ; pharyngobranchial 1 is rod-like. Medial to the lobe, epibranchials 1 and 2 are connected ventrally by tuberculate tissue forming a sessile pad. Microbranchiospines externally and internally on the three posterior gill arches.

The lower pharyngeal tooth plate (Fig. 3) is very elongated with deeply incised posterior margin. The teeth are long, narrow and pointed. Anteriorly and along lateral margins with rounded bases, apically narrower and feebly antrorse : medially and caudally with bases a little compressed laterally, with one or two blunt low anterior points and strong antrorse posterior point. No tooth plates on ceratobranchial 4.

Vertebrae 16+14 = 30(3), 16+15 = 31(1) ; four anterior vertebrae distinctly compressed ; the length of the abdominal vertebral column equals the caudal without the last vertebra. No ribs on caudal vertebrae. No tooth plates on ceratobranchial 4.

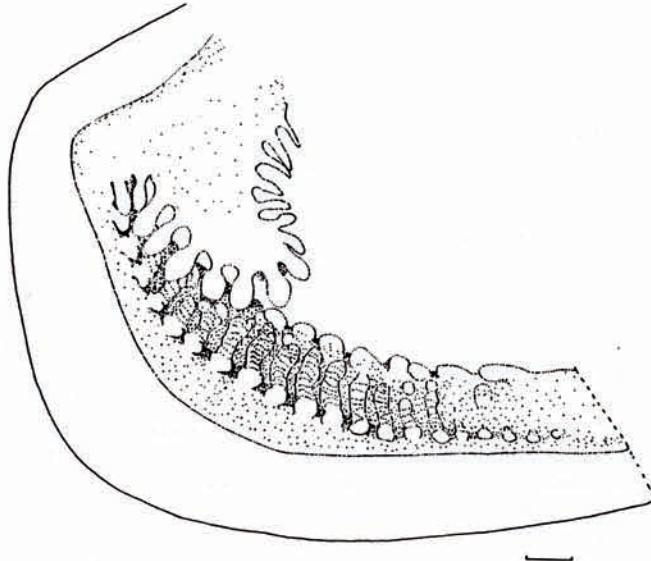


Fig. 2 : *Satanoperca lilith*. Lateral aspect of first gill arch. Scale : 1 mm. From ISBN 759. 71.6 mm SL.

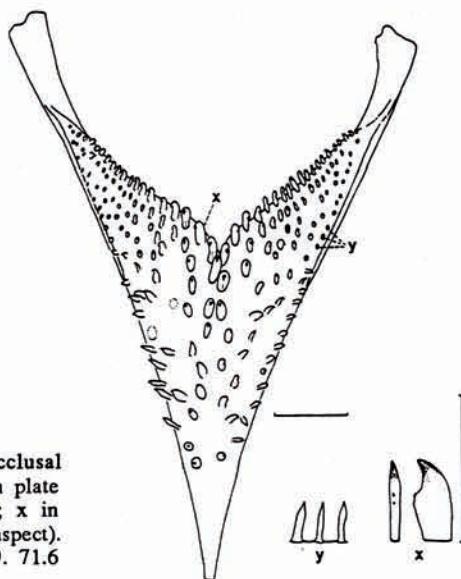


Fig. 3 : *Satanoperca lilith*. Occlusal aspect of lower pharyngeal tooth plate and teeth (y in lateral aspect ; x in rostral (left) and medial (right) aspect). Scales : 1 mm. From ISBN 759. 71.6 mm SL.

**Colouration :** Specimens over 100 mm with ground colour yellowish white on belly, preventrally, underside of head, along anal fin base and on lower margin of caudal peduncle. Branchiostegal membrane margin laterally greyish white. Countershaded, back and upper margin of caudal peduncle greyish brown, sides light brownish, ventrally with light intramarginal scale margins.

Snout dorsally, upper lip, posterior part of lower lip, and preorbital greyish brown; cheek more brownish. Brown stripe continuing anterior margin of preorbital to preoperculum. Operculum and suboperculum greyish.

Black, round or ovate blotch across lateral line scales 11-13; more ovate and

with center on lateral line tubes in specimens up to size of holotype, rounded and with center above lateral line tube row in larger specimens. Blackish stripe obliquely forwards across nape from posterior margin or just behind upper margin of orbit. Across the forehead three indistinct dark stripes, one directly intraorbitally, before that one forwards curved between the orbits, and above the nostrils bilateral disconnected elongate spots. Two dark, very faint parallel stripes on lacrimal, from eye to each lateralis canal opening on labial margin. No dark spots on cheek or gill cover.

Dorsal fin pale greyish to brownish with blackish lappets. Large round whitish spots on spinous portion, at most three on a particular membrane, and, more distinct, on eight last soft part membranes (up to six spots). Anal fin similar or lighter, but immaculate or with only indications of spots on last few membranes. Caudal fin basally like the body, distally pale brown grey, ventral lobe immaculate, dorsal lobe immaculate or, in large specimens, with up to five large round white spots along each membrane. Slightly behind caudal fin base, above lower lateral line level, a blackish brown spot with white ring. The caudal ocellus varies in position between middle and upper half of dorsal lobe, and may be double as well as having the nuclear dark spot greatly reduced in size. Pelvic fin white, anterior half dusky or greyish brown, first ray outer margin white.

Faint, slightly forwards (ventral) inclined, narrow vertical bars show better in young (less than 100 mm), overall lighter specimens. (1) rather a spot around the dorsal fin origin. (2) below dorsal fin anterior to the third bar. (3) containing the midlateral blotch, over lateral line scales 11 or 12 to 13. (4) below the soft dorsal fin. (5) from the end of the soft dorsal fin. The bars are more or less connected on the back and do not reach below the level of the lower edge of the pectoral axilla. The distinct stripe across the nape is more or less continuous with a small dark spot immediately behind the eye. In the specimens about 200 mm, a wide shadow below lower lateral line from the caudal fin base, forwards paralleling the ventral body contour at some distance from it, to the pectoral axilla; with short extensions dorsad, to the midlateral blotch, behind the midlateral blotch, and up behind the end of the upper lateral line (this one with indication of intensification behind the upper lateral line).

**Distribution (Fig. 4) :** Collecting localities range along the Amazon from

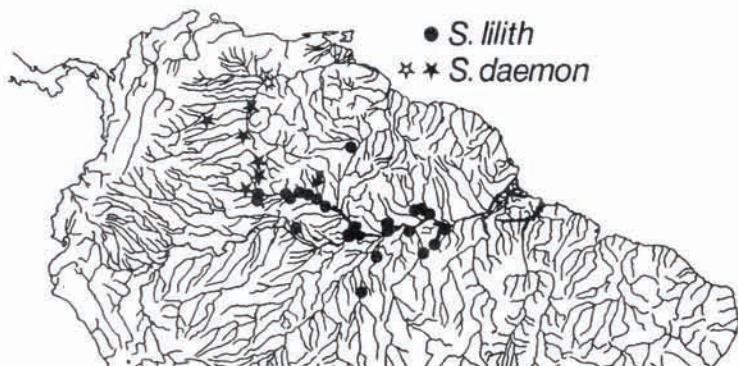


Fig. 4 : Collecting localities of *Satanoperca lilith* and *S. daemon* (open stars are literature records). Arrow indicates type locality of *S. lilith*.

Lago Amanã on the Rio Japurá, a tributary of the Rio Solimões, to the lower Rio Tapajós, a tributary of the Rio Amazonas. The species also ascends the Rio Trombetas, Rio Branco, Rio Canumã and the Madeira tributary Rio Aripuanã, and ranges along the Rio Negro from the Rio Curucuriari to the mouth region.

**Feeding ecology :** Stomach contents of *S. lilith* from the Rio Negro showed that insects and crustaceans were the principal food items during high water levels and that plant matter and insects were the principal food items during low water levels (Table III ; Fig. 5). The predominant insects were aquatic immature forms

Table III : Stomach contents of *Satanoperca lilith* and *S. jurupari* from the Rio Negro : Mean volume (MV, %), Relative occurrence (RO, %), and Feeding index (FI, %) during high and low water seasons.

	<i>Satanoperca lilith</i>						<i>Satanoperca jurupari</i>					
	High water			Low water			High water			Low water		
	MV	RO	FI	MV	RO	FI	MV	RO	FI	MV	RO	FI
No of stomachs analysed	11			37			15			26		
No of stomachs with food	11			37			15			25		
	HV	RO	FI	HV	RO	FI	MV	RO	FI	MV	RO	FI
Plant matter	8.6	45.5	5.0	24.6	89.2	28.0	27.3	60.0	24.0	17.1	72.0	15.0
Crustaceans	27.0	90.9	30.0	9.3	54.1	6.0	16.6	60.0	15.0	5.0	64.0	4.0
Insects	37.5	100.0	46.0	19.0	89.2	22.0	8.3	53.3	7.0	8.3	72.0	8.0
Other arthropods	0.5	18.2	0	-	-	-	0.5	13.3	0	0.2	12.0	0
Molluscs	4.6	27.3	0.1	-	-	-	-	-	-	-	-	-
Fishes	11.2	81.8	11.0	16.7	73.0	16.0	38.3	86.7	49.0	44.0	84.0	46.0
Sand grains	2.2	9.1	0	15.7	81.1	16.0	0.5	13.3	0	2.4	36.0	1.0
Unidentified matter	8.4	54.5	7.0	14.7	64.9	12.0	8.5	40.0	5.0	23.0	88.0	25.0

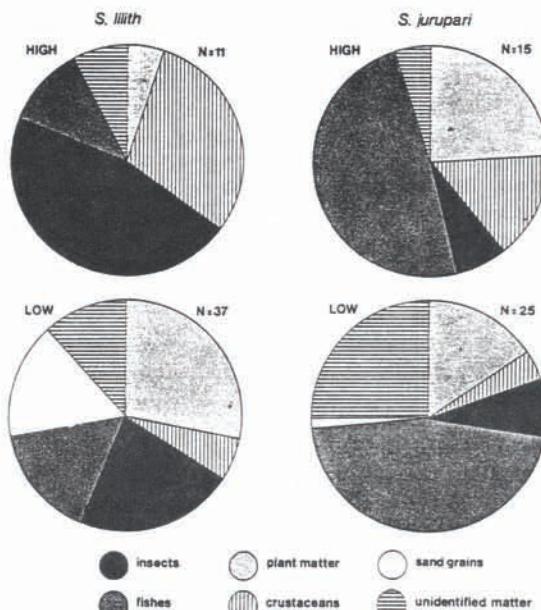


Fig. 5 : Diagram of stomach contents, based on feeding index, of *Satanoperca lilith* and *S. jurupari* from the Rio Negro during both high and low water levels. See also Table III .

of Diptera, Coleoptera and Trichoptera. Ostracoda, Cladocera and Conchostraca were the main crustaceans. Pieces of leaves made up plant matter. Fish scales were also found, and it is very probable that these were picked up from the bottom of the river rather than taken directly from fishes.

**Etymology :** *Lilith* (Hebrew) was Adam's first wife in Near East folklore; more generally in European and Near East folklore a female demon. The name is given in allusion to the close relationship to *Satanoperca daemon* (*daemon* from the Greek *daimon* or *daimonion*, divine being, demon).

## DISCUSSION

The genus *Satanoperca* now includes six valid species. The Amazonian *Satanoperca jurupari* is redescribed by Kullander (1986) on the basis of western Amazonian material. A redescription of the Guianan *S. leucosticta* has been prepared (Kullander and Nijssen, ms). *Satanoperca jurupari*, *S. leucosticta* and *S. pappaterra*, and all undescribed forms known to us, are readily distinguished from *S. lilith* by lacking flank spots, having lower scale and vertebral counts and having dorsal fin count modes XV.10 or XVI.9 instead of XIV.13.

Gosse (1976) confused *S. lilith*, *S. daemon* and *S. acuticeps* (Heckel, 1840). These species differ from all other *Satanoperca* species in possessing one to three dark blotches on the side and in having long, free, filamentous soft rays in the dorsal fin (Table I). *Satanoperca daemon* has been collected in the Rio Orinoco drainage and in the upper Rio Negro drainage upstream from the Rio Uaupés. *Satanoperca acuticeps* is restricted in distribution to central Amazonia, including the lower Rio Negro and the lower Rio Branco.

*Satanoperca daemon* and *S. lilith* are distinguished as a group by their larger size and higher meristics (Table I). There are no obvious morphometric or meristic differences between these species in the material compared. There are, however, discrete differences in the colour pattern.

In *S. daemon* there are always two rounded or vertically oval flank blotches. The anterior corresponds in position to the single blotch in *S. lilith* though the entire blotch or at least its core portion remains at all sizes below the lateral line canal row. The posterior blotch is also situated below the level of the upper lateral line, either below its terminal scales or posterior to the upper lateral line. The position of the anterior blotch below rather than on or above the upper lateral line, and the presence of one more blotch at the end of the upper lateral line thus distinguishes *S. daemon* from *S. lilith*.

Adult *S. daemon* also have a, usually interrupted, brown line on the cheek running closely along the infraorbitals and lacrimal, and also scattered brown spots on the gill cover. These spots are apparently iridescent blue in life and are not found in *S. lilith*.

Having a single large dark spot on the side is a common feature of South American cichlids. It might thus seem that the single spot in *S. lilith* represents the ancestral state compared to the two-blotched or three-blotched condition. There is, however, an interesting morphcline within *Satanoperca*, the polarity of which is not evident.

(1) *Satanoperca acuticeps* has three flank blotches along the middle of the side, each blotch situated close above the level of the lower lateral line, and a caudal ocellus also situated close above the lower lateral line level. In (2) *S. daemon* the anteriormost flank blotch has disappeared and the remaining two as well as the

caudal fin ocellus are slightly more dorsal in position. A trace of the anteriormost flank blotch is occasionally present in the form of a curved, faint stripe reaching to the dorsal fin base. In (3) *S. lilith* the single remaining flank blotch, corresponding to the middle blotch in *S. acuticeps*, is situated on or above the upper lateral line. In (4) *S. jurupari* and similar species, finally, there are no flank blotches and the relatively small caudal ocellus is situated close to the extreme dorsal margin of the caudal fin. *Satanoperca jurupari* group species generally have the sides plain or show a more or less distinct pattern of vertical bars and a lateral band in about the same position as the row of flank blotches in *S. acuticeps*.

*Satanoperca acuticeps* is variable in colour pattern, often having the flank blotches almost faded. *Satanoperca acuticeps* also differs from all other *Satanoperca* species in snout shape and dentition. The mouth is terminal, with the snout tip at level of the horizontal axis of the body, whereas in the other *Satanoperca* species the mouth is low, well below the midaxis of the body. The lower lip fold is continuous, whereas in the other species it is interrupted symphysially. The upper jaw dentition is biserial, unlike in the other species which have virtually always uniserial upper jaw dentition. The differences in mouth shape and dentition probably reflect food differences. *Satanoperca acuticeps* probably takes pelagic food and the other species are probably bottom or substrate feeders. Nevertheless, the pharyngeal jaw and gill arch morphology is similar in all *Satanoperca* species.

The stomach data of *S. lilith* from the Rio Negro (Table III, Fig. 5), with its significant inclusion of sand particles during the low water season suggest that this species is a benthivore. Stomach contents of *S. jurupari* from the Rio Negro showed fish and plant matter to be the principal food items during both high and low water levels (Table III, Fig. 5). Scales and pieces of fishes were the main fish items during the high water level, and scales and young cichlids (not *Satanoperca*) during the low water season. The plant matter was composed mainly of fruits and seeds during the high water levels and pieces of leaves during the low water season. The small quantity of sand found in the stomachs suggest that this species may not be a bottom feeder, but rather a substrate feeder feeding among floating or submersed aquatic macrophytes. There are as yet no stomach data available for *S. acuticeps*.

*Satanoperca pappaterra*, *S. jurupari*, and similar species that are identified as *S. jurupari* by aquarists, are mouth brooders (Kullander, 1986; Peters and Berns, 1982; Stawikowski and Werner, 1988). The only report of successful breeding in captivity of *S. daemon* (Eckinger, 1987; Stawikowski and Werner, 1988) suggests that this species is a biparental substrate brooder. The reproductive behaviour of *S. acuticeps* and *S. lilith* is still unknown.

Gosse's (1976) material of *S. daemon*, of which was reexamined a part only, seems for the most part to consist of *S. lilith*. The holotype, the ISBN 17415 sample from the Rio Uaupés (reexamined) and probably the Caño de Quiribana material (not reexamined) are *S. daemon*, whereas the other 19 lots are actually or probably *S. lilith*, some of them here included in the type series of *S. lilith*. Earlier, Steindachner (1875) also identified specimens of *S. lilith* as *S. daemon*. Gosse remarked that certain specimens possessed a second spot at the end of the upper lateral line, but both Gosse and Steindachner obviously considered a single spot at the middle of the side as characteristic of the species.

The holotype of *S. daemon*, NMW 23123, is a 233.0 mm specimen collected by J. Natterer probably at Marabitanas on the upper Rio Negro in February 1831. It is now in a poor state of preservation, soft and completely discoloured, and has extensively damaged squamation and finnage. It has the dorsal fin count XIV.12, anal fin count III.8, pectoral fin rays 14, scales in a lateral row 30. Whereas by size and meristic characters it must belong to one of the two *Satanoperca* species with one or two flank blotches it seems hardly possible to identify this specimen as belonging

to either. However, Heckel's diagnosis and description clearly indicate that the specimen had two flank spots, one on the middle and one at the end of the upper lateral line ('Maculis duabus in parte superiore linea lateralis, altera in medio, altera terminali,...'), and also considering the locality, Marabitanas, which is within the range of the two-blotched *Satanoperca*, it is obvious that the upper Orinocoan-upper Negro species is *S. daemon*.

*Satanoperca daemon* and *S. lilith* have complementary distributions (Fig. 4). Sympatry in the upper Rio Negro drainage cannot be dismissed from consideration because that region is still far from well collected. The distribution pattern nonetheless indicates that the upper Rio Negro has had a history different from that of the rest of the Rio Negro. Several other cichlid species show a similar distribution pattern although little has been published so far, hampering further discussion here.

*Satanoperca lilith* is kept as aquarium fish, usually then handled as *S. daemon*. Aquarists have recognized that two forms or species are involved, however. Popular descriptions and photos of *S. lilith* have been published recently by Staack and Linke (1985, p. 128) and Stawikowski and Werner (1988, p. 188).

#### Key to *Satanoperca* species

- 1 - Scales in a lateral row 29-31, circumpeduncular scale rows 20.....2
- Scales in a lateral row 27-28, circumpeduncular scale rows 16.....3
- 2 - A single dark blotch on side, situated across upper lateral line.....*S. lilith*
- Two dark blotches on side, situated below upper lateral line.....*S. daemon*
- 3 - Three dark blotches along side, all below upper lateral line, lower lip fold continuous.....*S. acuticeps*
- No dark blotches on side, lower lip fold discontinuous anteriorly.....*S. jurupari* group.

**Acknowledgements :** Museum material used in this paper was placed at our disposal by Michael Goulding, Harald Ahnelt, the late Rainer Hacker, Richard P. Vari, Heraldo Britski and Jean-Pierre Gosse. Anita Hogeborn-Kullander made the photograph (Fig. 1). Financial support was provided by the Swedish Natural Science Research Council grant no. B-BU 4568-108 to SOK.

#### REFERENCES

- ECKINGER D., 1987. - Nachzucht von "Geophagus" *daemon*. *DCG-Informn*, 18 : 132-134.  
 FERREIRA E.J.G., 1984. - A ictiofauna da represa hidrelétrica de Curuá-Una, Santarém, Pará. II - Alimentação e hábitos alimentares das principais espécies. *Amazoniana*, 9 : 1-16.  
 GOSSE J.-P., 1976. - Révision du genre *Geophagus*. *Mém. Acad. r. Sci. Outre-mer. Cl. Sci. Nat. méd. (N.S.)*, 19(3) : 1-172.  
 HECKEL J., 1840. - Johann Natterer's neue Flussfische Brasilien's nach den Beobachtungen und Mittheilungen des Entdeckers beschrieben. (Erste Abtheilung, die Labroiden). *Annl wien. Mus. Natges.*, 2 : 327-470.  
 KULLANDER S.O., 1980a. - A taxonomical study of the genus *Apistogramma* Regan, with a revision of Brazilian and Peruvian species. *Bonn. zool. Monogr.*, 14 : 1-152.  
 KULLANDER S.O., 1980b. - A redescription of the South American cichlid fish *Papiliochromis ramirezi* (Myers & Harry, 1948). *Stud. neotrop. Fauna Envir.*, 15 : 91-108.  
 KULLANDER S.O., 1986. - Cichlid fishes of the Amazon River drainage of Peru. Stockholm, 431 pp.  
 KULLANDER S.O. & H. NIJSSEN, ms. - The cichlids of Surinam.  
 PETERS H.M. & S. BERNS, 1982. - Die Maulbrütpflege der Cichliden. Untersuchungen zur Evolution eines Verhaltensmusters. *Z. zool. Syst. Evolvorsch.*, 20 : 18-52.  
 STAACK W. & H. LINKE, 1985. - Amerikanische Cichliden II. Grosse Buntbarsche. Melle, 164 pp.

- STAWIKOWSKI R. & U. WERNER, 1988. - Die Buntbarsche der Neuen Welt. Südamerika.  
Essen, 288 pp.
- STEINDACHNER F., 1875. - Beiträge zur Kenntniss der Chromiden des Amazonenstromes. *Sber.  
k. Akad. Wiss. Wien Math.-Natw. Cl.*, 71 : 61-137.

*Reçu le 20-03-1988.*

*Accepté pour publication le 20-06-1988.*